

Multiple Cues in Status Signalling: The Role of Wingbars in Aggressive Interactions of Male House Sparrows

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Abstract

During aggressive interactions, animals may signal their competitive ability by various ornaments referred to as badges of status. The use of a single badge predicting dominance rank occurs in many vertebrate species. However, animals often display multiple ornaments that may convey information about either different or the same aspects of the signaller's quality, or alternatively, may serve as signal amplifiers. We observed the fighting behaviour of male house sparrows in two captive flocks to investigate whether they may use multiple cues in status signalling during aggressive interactions. Beside the status-signalling bib, male sparrows possess a conspicuous white wingbar that they often display upon aggressive encounters. We tested whether bib size and the wingbar's conspicuousness (i.e. its achromatic contrast with the neighbouring dark feathers) or its area predicted success in various aspects of fighting. We found that bib size strongly predicted overall fighting success (i.e. proportion of fights won) and defence success (i.e. proportion of successful defences out of all attacks received). Wingbar conspicuousness was positively related to defence success after controlling for the effect of bib size in multivariate analyses. Furthermore, displaying the wings also tended to improve the birds' success in defence but not in attack. Wingbar area was unrelated to any measured aspect of fighting ability. We suggest that bib size and wingbar conspicuousness may convey multiple messages on fighting abilities, specifically on overall aggressiveness and defending potential, respectively. Alternatively, wingbars may serve as amplifiers for the wing displays of aggressive motivation. Thus, male sparrows may use multiple cues in assessing the competitive ability of opponents during social interactions.

Introduction

The status signalling hypothesis (Rohwer 1975) proposes that conspicuous colour traits have evolved to signal differences in the ability to win agonistic contests. Signalling fighting abilities or aggressiveness should be advantageous for all participants, as they may assess the expected outcome of the fight and may therefore avoid costly and unnecessary interac-

tions (Rohwer 1975). Several studies have found a relationship between coloration and dominance status in diverse vertebrate species including birds (reviewed by Senar 1999) and lizards (reviewed by Whiting et al. 2003). Such colour traits were termed 'badges of status' as they were considered cheap to produce and potentially open to cheating. However, recent studies increasingly suggest that certain colour badges are costly to produce and/or to maintain

(Gonzalez et al. 2001, 2002; McGraw et al. 2003; Török et al. 2003, reviewed by Jawor & Breitwisch 2003), so it may only pay high-quality or highly motivated individuals to signal high status (Enquist 1985, reviewed by Johnstone 1995). Although animals often exhibit several conspicuous ornaments, previous studies have almost exclusively focused on single badges of status.

Multiple ornaments have received increasing research interest rather in the context of sexual signalling and mate choice (reviewed by Candolin 2003). Most of these studies found multiple ornaments to function either as 'multiple messages' that reflect different aspects of individual quality or as 'backup signals' that allow a more accurate assessment of a single aspect of quality (Candolin 2003). Evidence also increases for 'uninformative cues' that do not indicate qualities per se but facilitate the detection and assessment of an indicator trait (Candolin 2003). Such interactions among cues of individual quality may also be advantageous during status signalling in competition for resources other than mates, such as for food in wintering flocks of birds. Although a few studies raised the possibility of multiple status signals (Balph et al. 1979; Zucker 1994; but see Zucker & Murray 1996), these were not of strong support and left the topic open for debate.

One of the best-studied species with a status signalling system is the house sparrow (*Passer domesticus*). In winter flocks of house sparrows, the size of males' black throat patch (the bib) predicts their dominance rank (Møller 1987; Solberg & Ringsby 1997; Liker & Barta 2001; Gonzalez et al. 2002; Hein et al. 2003). Beside the bib, male sparrows exhibit several other contrastingly coloured plumage patches, including a conspicuous wingbar formed by light tips on the median coverts. The wingbars may be flashed by slightly spreading the wings, or totally hidden by ruffling the flank feathers. When competing for food, sparrows frequently use a threatening posture (wing display henceforward) in which they spread and wiggle their wings (Perrins 1998) that appear to emphasize the wingbars. This behaviour suggests that wingbars may be involved in signalling to opponents during aggressive interactions.

Many other bird species also exhibit light wing patterns (Price & Pavelka 1996), and several functions have been found for such ornaments in various taxa, from distracting prey (Jablonski 1996) or predators (Brooke 1998) through facilitating flock cohesion (Beauchamp & Heeb 2001) to sexual selection

by female choice (Senar et al. 2005). Displaying the wings during aggressive encounters is also widespread among birds (Perrins 1998; Hurd & Enquist 2001), and some studies on various avian species have suggested that white wingbars might signal individual quality in intra-sexual competition in males (Jablonski & Matyjasiak 2002; Török et al. 2003) and females (Ruusila et al. 2001). However, the function of the wingbars has not been tested in house sparrows.

In this study, we investigated the role of the wingbars and wing displays in aggressive interactions among male house sparrows. Specifically, we asked whether these traits may act as multiple cues in status signalling, that is, do they in addition to bib size predict any aspect of fighting success. Firstly, we tested whether males with larger and/or more conspicuous wingbars are more successful in social competition among conspecifics in winter flocks than less ornamented males. Secondly, we examined whether the use of wing display is related to success in different aspects of fighting behaviour.

Methods

Study Subjects

We captured 28 house sparrows using mist nets in Nov. 2003 in the Budapest Zoo, Hungary. After capture, we immediately measured body mass (± 0.1 g), tarsus (± 0.1 mm) and wing length (± 1 mm), and ringed all birds with a numbered metal ring and an individual combination of three colour rings. We then formed two mixed-sex flocks consisting 15 and 13 individuals, respectively (male:female ratios were 9:6 and 10:3). House sparrows live in mixed-sex flocks year-round, and sexes do not differ in dominance rank or aggressiveness (Liker & Barta 2001; Hein et al. 2003). Flocks were housed in two indoor aviaries measuring 3 m (W) \times 4 m (L) \times 2 m (H) and 2 m (W) \times 3 m (L) \times 2 m (H), separated so that individuals of different flocks could not interfere with each other. Both aviaries were lit by artificial light (9L:15D) and contained a feeding board for presenting food, artificial roosting trees and small boxes for sleeping and resting. Food, water, sand and fine gravel (to facilitate digestion) were provided ad libitum. Food consisted of a mixture of seeds and occasionally mealworms. After the study, we released the birds at the site of capture. Released birds were in good condition and apparently re-established themselves in the local population, as we often re-encountered them after the release

(Á. Z. Lendvai, pers. obs.). The study was licensed by the Duna-Ipoly National Park (847/3/2003).

Aggressive Interactions

Behavioural observations were conducted between Nov. 2003 and Feb. 2004. During the observations, we recorded aggressive encounters between pairs of individuals when both participants were identified and the outcome of the contest was straightforward. We recorded 1050 dyadic fights in which one or both participants were males. An individual was considered to win a fight if it clearly supplanted the opponent. For each male, we calculated overall fighting success, i.e. the number of wins divided by the total number of aggressive encounters which the focal bird was involved in (a measure that strongly correlates with dominance rank; Liker & Barta 2001). Then, we calculated two additional components of fighting success: (1) attack success, i.e. the proportion of successful attacks out of all attacks launched by the focal bird, and (2) defence success, i.e. the proportion of successful defences out of all attacks received by the focal bird. Measuring success between opponents in established flocks is a standard method to test the relationship between candidate status signalling traits and fighting ability or aggressiveness of individuals (e.g. Møller 1987; Solberg & Ringsby 1997; Liker & Barta 2001; Hein et al. 2003).

To study wing displays, we videorecorded the birds' behaviour in each flock on two occasions during the first feeding in the morning. Before the recordings, we placed six clumps of millet seeds on the feeding board. Trials lasted until the food clumps were depleted and the birds left the feeding board. We analysed a total of 32 min video recordings for the two flocks. In these recordings, we identified 116 aggressive interactions in which one or both participants were males. For these interactions, we recorded the aggressor and the winner, and noted whether participants used wing display. We defined wing display as flapping or wobbling the wings towards the opponent during fights (we excluded wing movements associated with flight). For all males ($n = 19$), we calculated attack success and defence success (as above) separately for interactions with and without wing display.

Measuring Coloration

Before releasing the birds, we took digital photographs from each male to measure their bib size and

the conspicuousness and area of their wingbars. Birds were held in standard position and were photographed in a standardized set-up with constant lighting conditions. Bibs were photographed with the birds' beak held perpendicular to body axis so that we could measure the so-called visible bib (Gonzalez et al. 2001). Wingbars were photographed on the left wings flattened. Photos were converted to grey-scale and measured using the SCION IMAGE software (Scion Corporation 1998). We selected the area of bib or wingbar using the 'density slice' and 'wand tool' functions. Areas were measured in pixels and converted to cm^2 using a measured standard in the photos. Brightness of the wingbar was measured as the mean density of the pixels constituting the wingbar on the photos (the lighter the pixel, the smaller the density value). We also measured the mean density of the area of brown lesser coverts above the wingbar. This area may serve as a natural background or 'standard' against which birds see and judge wingbars, as in threat displays sparrows rotate their wings so that lesser coverts point towards the opponent (Perrins 1998; pers. obs.). We calculated wingbar conspicuousness by subtracting wingbar density from lesser coverts density, and used this variable as a measure of wingbar conspicuousness (greater values may be interpreted as greater achromatic contrast between the wingbar and the lesser coverts). We preferred wingbar conspicuousness over wingbar brightness because conspicuousness depends not only on the brightness of the plumage patch, but also on its visual environment, and within-animal contrast may be a more objective measure of conspicuousness in most natural habitats of sparrows (Endler 1990).

We tested the reliability of our colour measurements in several ways. Firstly, we measured each photograph twice and calculated the repeatability of measurements (Lessells & Boag 1987). Repeatability proved very high for bib size ($r = 0.97$, $F_{18,19} = 64.3$, $p < 0.001$), wingbar area ($r = 0.78$, $F_{18,19} = 8.1$, $p < 0.001$) and wingbar conspicuousness ($r = 0.90$, $F_{18,19} = 19.7$, $p < 0.001$; see also Bókony et al. 2003 for further justification of area measurements from photos). Secondly, to validate our method using grey-scale density values as a proxy for wingbar conspicuousness, we plucked the 2–5th median coverts with white tips from 25 male sparrows captured at a different site, and measured their reflectances using a USB2000 spectroradiometer with a Mini-DT deuterium-halogen light source (Ocean Optics Europe, Duiven, The Netherlands; methods as in Cuthill et al. 1999). As these feathers did not

reflect in the UV, we calculated total reflectance for the 400–700 nm range of the spectra as an objective measure of wingbar brightness (Marchetti 1993; McNaught & Owens 2002). Before plucking the feathers, we took photographs of the birds' wingbars and measured the density values of these as described above. Wingbar density correlated significantly with total reflectance ($r = -0.49$, $p = 0.013$, $n = 25$; note that a negative correlation is expected as the greater the brightness, the lesser the density value).

Statistical Procedure

To explore the relationships between colour traits and measures of fighting ability in males, we used general linear models (GLM) with flock as a random factor and bib size, wingbar area and wingbar conspicuousness as covariates. Dependent variables (fighting success, attack success and defence success) were arcsine square-root transformed before the analyses. We used stepwise backward elimination of non-significant effects, by removing the predictor with the largest p -value in each step (Grafen & Hails 2002). We do not report flock effects as these were non-significant in all models, and there were no significant interactions between the flock factor and other predictor variables. As tarsus and wing length and body mass were unrelated to measures of both coloration and fighting ability in our sample (results not shown) and also in other studies (e.g. Møller 1987; Liker & Barta 2001), we did not control for these biometrical variables in the analyses.

As the power of our tests was low because of small sample sizes, we did not use any corrections of significance levels for multiple comparisons, as these would only exacerbate the problem of low power by increasing the risk of neglecting existent small effects (Nakawaga 2004). Instead, to prevent our conclu-

sions from being based purely on the significance of each test, we also evaluated our results using a different analytical approach, the information-theoretic model comparison (Anderson et al. 2000), where inference is based on the entire model set. We evaluated all possible subsets of the three initial GLM models based on the second-order Akaike's information criterion corrected for small sample size (AICc). As no single model was highly superior compared with the others in our model sets, we performed model-averaging (Anderson et al. 2000), where model coefficients were weighted using Akaike weights. We also examined the relative importance of predictors by summing the Akaike weights for each predictor across all sub-models that contained that predictor. Then, we compared the final sets of predictor variables selected in each approach (i.e. stepwise GLM and AICc-based model-averaging).

We analyzed the data on display behaviour using the independent sample derived from video recordings. Here, we used non-parametric tests because the distribution of these variables did not allow for parametric tests. Using Wilcoxon's matched-pairs signed-ranks tests, we tested whether the males' attack success and defence success were greater when displaying than when not displaying. As the power of these tests were low because of the small number of males performing attacks and defences both with and without wing display in our sample, we also checked for the associations between success and display using fights as data points in χ^2 -tests. As these data points are not independent (each male participated in several fights), in this latter case we used a full permutation procedure to calculate the exact level of significance for the tested associations.

All statistical tests were two-tailed with a 95% CI. We used the R statistical computing environment (R Development Core Team 2003) and SPSS for Windows 12.0 for statistical analyses.

Table 1: Relationships of plumage colour traits with measures of fighting ability in male house sparrows using stepwise GLMs. Predictor variables are bib size (B), wingbar conspicuousness (C), and wingbar area (A). Asterisks (*) indicate predictors included in the final models. For these variables, regression coefficients (b) \pm SE and effect sizes (η^2) are given for the final models. For predictors not included in the final models, estimates are given for the initial models

Predictor	Fighting success ^a		Attack success		Defence success ^b	
	$b \pm SE$	η^2	$b \pm SE$	η^2	$b \pm SE$	η^2
B	0.10 \pm 0.04	0.274*	0.04 \pm 0.04	0.055	0.09 \pm 0.03	0.416*
C	0.01 \pm 0.01	0.189	0.01 \pm 0.01	0.098	0.01 \pm 0.004	0.381*
A	-0.01 \pm 0.24	<0.001	0.01 \pm 0.24	<0.001	-0.20 \pm 0.16	0.096

^aFinal model: $F_{1,17} = 6.42$, $p = 0.021$.

^bFinal model: $F_{2,16} = 13.97$, $p < 0.001$.

Results

Wingbar area and wingbar conspicuousness were not correlated (Pearson's correlation, $r = -0.05$, $p = 0.828$, $n = 19$). Bib size was not correlated with wingbar area ($r = 0.37$, $p = 0.120$, $n = 19$) or wingbar conspicuousness ($r = 0.24$, $p = 0.324$, $n = 19$). Defence success and attack success were significantly correlated ($r = 0.68$, $p = 0.001$, $n = 19$).

Coloration and Fighting Ability

Bib size was the strongest predictor for each measure of fighting ability both in stepwise GLMs (Table 1) and AICc-based model comparison (Tables 2 and 3). For fighting success and defence success, both the final GLM (Table 1) and the models with the lowest AICc included bib size (Table 2). For attack success, the best model contained bib size again, but its relative importance was similar to that of the other coloration variables (Table 3), and its effect was non-significant in GLM (Table 1).

Wingbar conspicuousness was significantly related to defence success only; both the final GLM (Table 1) and the model with the lowest AICc (Table 2) for defence success included wingbar conspicuousness in addition to bib size. Both traits were of similar importance in explaining defence success, as indicated either by effect size in GLM (Table 1) or the sum of Akaike weights (Table 3).

Wingbar area was not related to any measures of fighting ability in GLMs (Table 1) and proved of minor importance in AICc-based model selection (Table 3).

Wing Displays

In the video samples, defence success tended to be greater when the defender's wingbar was displayed than when it was not (Wilcoxon's matched-pairs signed-ranks tests, $Z = -1.49$, $p = 0.068$, $n = 8$ males, Fig. 1), while attack success was not improved by wing displaying ($Z < 0.001$, $p > 0.999$, $n = 7$ males). When we used fights as data points, success was significantly associated with the use of wing display in defences ($\chi^2_1 = 16.36$, $n = 63$ defences, exact $p < 0.001$), but not in attacks ($\chi^2_1 = 1.06$, $n = 91$ attacks, exact $p = 0.388$).

Discussion

In this study, we demonstrated that male house sparrows may use multiple cues in status signalling

Table 2: Model selection based on Akaike's information criterion corrected for small sample size (AICc): AICc values, number of estimated parameters (K), AICc differences between the best model and each candidate model (Δ_i), and Akaike weights (ω_i) of the candidate models are given for measures of fighting ability

Dependent	Model	Predictors	AICc	K	Δ_i	ω_i
Fighting success	1	B	1.04	3	0.00	0.41
	2	B + C	1.98	4	0.94	0.26
	3	C	3.15	3	2.10	0.14
	4	B + A	4.23	4	3.19	0.08
	5	A + C	5.72	4	4.67	0.04
	6	B + A + C	5.74	5	4.70	0.04
	7	A	6.99	3	5.94	0.02
	8	B + F	15.01	4	13.97	0.00
	9	A + F	16.56	4	15.52	0.00
	10	B + A + F	19.66	5	18.62	0.00
	11	C + F	20.69	4	19.65	0.00
	12	B + C + F	24.77	5	23.73	0.00
	13	A + C + F	24.91	5	23.87	0.00
	14	B + A + C + F	30.18	6	29.14	0.00
Attack success	1	B	0.27	3	0.00	0.36
	2	C	1.08	3	0.81	0.24
	3	A	1.74	3	1.47	0.17
	4	B + C	3.12	4	2.85	0.09
	5	B + A	3.53	4	3.26	0.07
	6	A + C	4.08	4	3.81	0.05
	7	B + A + C	6.87	5	6.60	0.01
	8	A + F	12.08	4	11.80	0.00
	9	B + F	13.93	4	13.65	0.00
	10	C + F	17.81	4	17.54	0.00
	11	B + A + F	18.72	5	18.45	0.00
	12	A + C + F	22.59	5	22.31	0.00
	13	B + C + F	25.06	5	24.78	0.00
	14	B + A + C + F	30.49	6	30.22	0.00
Defence success	1	B + C	-13.83	4	0.00	0.71
	2	B + A + C	-11.59	5	2.24	0.23
	3	B	-6.85	3	6.98	0.02
	4	B + A	-6.58	4	7.25	0.02
	5	C	-5.21	3	8.62	0.01
	6	A + C	-2.02	4	11.82	0.00
	7	B + F	6.90	4	20.73	0.00
	8	B + A + F	10.20	5	24.03	0.00
	9	C + F	11.73	4	25.56	0.00
	10	B + C + F	11.75	5	25.58	0.00
	11	A	11.99	3	25.82	0.00
	12	A + F	12.49	4	26.33	0.00
	13	B + A + C + F	16.51	6	30.34	0.00
	14	A + C + F	16.97	5	30.80	0.00

Predictor variables are bib size (B), wingbar conspicuousness (C), wingbar area (A) and flock (F).

during social competition. Firstly, we found that bib size of males was related to their fighting success. This finding agrees with other observations and experimental studies showing that bib size functions as a status signal during aggressive interactions of sparrows (Møller 1987; Solberg & Ringsby 1997;

Table 3: Model-averaged regression coefficients (b) and their unconditional SE for bib size (B), wingbar conspicuousness (C), and wingbar area (A) in relation to measures of fighting ability. Coefficients of a given predictor were weighted using the Akaike weight of each candidate model containing that predictor. Σ shows the sum of Akaike weights for each predictor across all models that contain that predictor, reflecting the relative importance of predictors in explaining variation in the dependent variable. The effect of flock as a random factor was not estimated

Predictor	Fighting success		Attack success		Defence success	
	Σ	$b \pm SE$	Σ	$b \pm SE$	Σ	$b \pm SE$
B	0.79	0.08 ± 0.17	0.53	0.03 ± 0.10	0.99	0.09 ± 0.09
C	0.48	0.01 ± 0.05	0.39	0.00 ± 0.03	0.96	0.01 ± 0.07
A	0.18	0.01 ± 0.11	0.31	0.02 ± 0.13	0.25	-0.05 ± 0.10

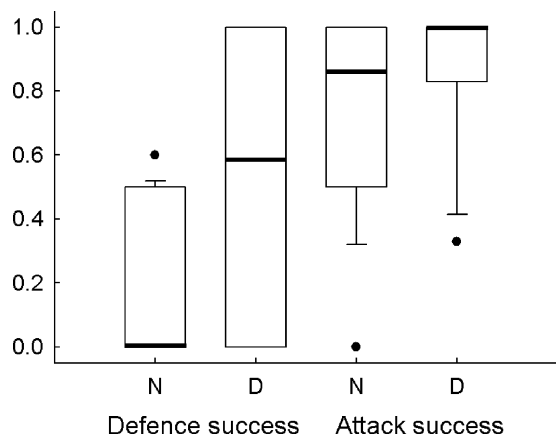


Fig. 1: Defence success and attack success of male house sparrows in aggressive interactions without wing display (N) and with wing display (D). Box plots show the medians (horizontal bar), 25th and 75th percentiles (top and bottom of box, respectively), 10th and 90th percentiles (whiskers) and outliers (dots). $N = 8$ and 7 males for defence and attack, respectively (see the text for statistics)

Liker & Barta 2001; Gonzalez et al. 2002; Hein et al. 2003). Secondly, we showed that beside bib size, the conspicuousness of the wingbar also explained a significant proportion of variation in defence success. This relationship was independent of the effects of bib size because (1) wingbar conspicuousness was unrelated to bib size in our sample, and (2) we controlled for the effects of bib size in multivariate analyses. Furthermore, we found that the use of wing displays also tended to improve the sparrows' success in defence, but not in attack. Thus, our results suggest that conspicuous wingbars may function in aggressive interactions of male sparrows by increasing the defence success of their bearer.

As bib size and wingbar conspicuousness were not correlated, it is unlikely that the wingbar is merely a back-up signal that serves to reinforce the signal of the bib. Furthermore, wingbar conspicuousness was

related to defence but not overall fighting success, suggesting that the bib and the wingbars may have different functions in signalling during aggressive interactions. Firstly, they may signal slightly different aspects of fighting ability. Namely, bib size may be important for assessing the opponents' overall aggressiveness or fighting ability (including both attacks and defences), whereas wingbar conspicuousness may specifically signal their ability to defend their already occupied resources (e.g. a food patch or resting site). In line with this idea, it has been shown in great tits (*Parus major*) that males selected for 'fast' exploratory behaviour attack their opponents more vigorously, but 'slow' individuals use more threat displays and they recover sooner after a defeat (Groothuis & Carere 2005), suggesting that attack and defence may involve different behavioural mechanisms. If such differences also exist in sparrows, it may pay for males to signal these different aspects of their fighting ability by different ornaments. Under this scenario, bib size and wingbar conspicuousness may act as 'multiple badges of status' in sparrows.

Alternatively, wingbars may not signal specific information about defending potential, but may serve as signal amplifiers (Hasson 1989; Candolin 2003) to facilitate the detection and/or assessment of the birds' wing displays. Avian wing displays probably signal aggressive motivation or willingness to escalate fights (Hurd & Enquist 2001). As sparrows can regulate the visibility of their wingbars either by exposing them in wing display or by hiding them with the neighbouring feathers, wingbars may function as 'coverable badges' (Hansen & Rohwer 1986) that are exposed when birds are highly motivated to defend their resources but not displayed when birds are not willing to engage in an escalated fight. Although sparrows use the wing display during both launching and withstanding attacks, it may be especially useful during defence because the level of motivation may be more variable among defenders

than among attackers. Attackers may usually be willing to fight (otherwise they would not attack), and accordingly, the majority of attacks result in wins in sparrows (Jawor 2000; this study: Fig. 1). Contrarily, defenders cannot help being attacked, and they should only risk fighting if they are motivated enough to defend their resources. This may explain our finding that wing displays increase defence success but do not affect attack success in sparrows. Birds may uncover their wingbars to amplify the signal of wing display, with more conspicuous badges being more effective threats (Hansen & Rohwer 1986).

We have found that the conspicuousness but not the area of wingbars was associated with defence success. This may reflect the fact that different characteristics of an ornament may differ in developmental constraints and/or selection pressures (Badyaev et al. 2001). For example, different aspects of a single plumage ornament in house finches (the hue of the red breast patch, its area and the symmetry of both) are partially independent of each other and differ both in proximate control and in fitness consequences (Badyaev et al. 2001). In sparrows, it is also possible that wingbar conspicuousness is a more reliable signal of defending ability or is more effective in amplifying rapid wing displays than the area of the wingbars (Endler 1990; Marchetti 1993).

In sum, we have found that in addition to the well-known bib size, the conspicuousness of the wingbar also relates to success in social competition in male house sparrows. Wingbar conspicuousness is specifically related to defence success, which is also improved by actively displaying the wingbars. We propose that the bib and the wingbar may convey multiple messages on aspects of fighting abilities or, alternatively, wingbars may serve as amplifiers for aggressive wing displays. To our knowledge, this is the first study to demonstrate a possible use of colour traits as multiple cues in non-sexual status signalling.

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